

Geographical variation and Pleistocene history of the *Erebia pandrose* – *sthennyo* complex (Nymphalidae; Satyrinae)

FRANS CUPEDO

Processieweg 2, NL-6243 BB Geulle, Netherlands; e-mail: frans@cupedo.eu

Abstract. The *Erebia pandrose-sthennyo* complex consists of two taxa: *pandrose*, with a Eurosiberian, arctic-alpine disjunct distribution, and *sthennyo*, hitherto considered a Pyrenean endemic. Their taxonomic status is uncertain because of their strictly allopatric distributions. The discovery of a *sthennyo*-like population in the Alps was cause for the present re-examination of the geographical distribution of typical *pandrose* and *sthennyo* characters, in 43 populations covering the whole geographic range of the *E. pandrose-sthennyo* complex. The investigated populations indeed split up into two taxonomical units, *pandrose* and *sthennyo*. The latter is not confined to the Pyrenees, but also inhabits the southeastern Alps, the Durmitor (Montenegro) and the southern Altai (Kazakhstan). No sympatric occurrence of *pandrose* and *sthennyo* was found. In the Alps, *pandrose* and *sthennyo* are separated by a belt of intermediate populations, resulting from intermingling in a zone of contact. Apparently they are not reproductively isolated. **Pleistocene history.** Both *pandrose* and *sthennyo* have a Eurosiberian distribution, resulting from spread in the glacial trans-palaearctic tundra belt, and subsequent shrink and disruption of the occupied area during interglacial times. As, however, *pandrose* and *sthennyo* are not reproductively isolated, they cannot have occupied the tundra simultaneously. Consequently their expansion has to be dated back to different glacial periods. Two arguments point to *sthennyo* as the first to have established its actual distribution: (i) The *sthennyo* populations of the Pyrenees, the Alps and the Altai show morphological differentiations, in wing design, wing shape, and in one genital character, whereas *pandrose* is uniform throughout its territory. The *pandrose* populations differ merely in the extent of *sthennyo* traits, resulting from former gene exchange. (ii) Today, *pandrose* is still inhabiting the northern region of the Alps, bordering the previous tundra zone, whereas *sthennyo* occupies refugial areas in the southern Alps, completely cut off from its former dispersion route. It is argued that the spread of *sthennyo* must date back to (at least) the Mindel glaciation (MIS8), and the spread of *pandrose* to (at least) the Riss period (MIS6). The main argument being that colonization of the Apennines (from the western Alps) and the Balkans (from the southern Carpathians) must date (at least) from the Würm glacial (MIS2-4), which implies that *pandrose* already lived in the Alps and the Carpathians during the Riss-Würm interglacial (MIS5). Scandinavian populations are completely intermediate. *Sthennyo*, present since the end of the Mindel glaciation, survived the Riss glaciation on the southern edge of the polar ice cap, where it interbred with *pandrose*. At the end of Riss, Scandinavia was repopulated by these mixed populations. **Taxonomy and nomenclature.** As *pandrose* and *sthennyo* are not reproductively isolated, they have to be considered conspecific. The hierarchical structure of *E. pandrose* is best reflected in taxonomy by creating two groups of subspecies, according to art. 6.2 of the ICZN, which should be named *Erebia pandrose (pandrose)* and *Erebia pandrose (sthennyo)*. Alpine and Scandinavian intermediate populations are arbitrarily placed in the *pandrose* group. Within the *pandrose* group, *ingana* Fruhstorfer, 1911 is shown to be a junior synonym (**syn. n.**) of *pandrose* (Borkhausen, 1788). Within the *sthennyo* group, *infraclara* Verity, 1953 is shown to be a junior synonym (**syn. n.**) of *marmolata* Dannehl, 1927. The South Altai population of the *sthennyo* group is described as *narymica* **ssp. n.**

Introduction

The geographical distribution pattern of oreo-tundral species is the result of repeated cycles of areal expansions and contractions, generated by Pleistocene climatic fluctuations (De Lattin 1967). During glacial times the arctic tundra shifted southwards, extending into a continuous trans-palaearctic belt between the polar ice sheet and the southern mountain systems (Pyrenees, Alps, Carpathians, Caucasus, and Altai). Not only tundral species, but also part of the populations inhabiting these mountain systems spread into the tundra. In many cases this led to oreo-tundral (arctic-alpine) disjunction, and/or to long-distance expansion in an east-west direction, resulting in a Eurasian dis-

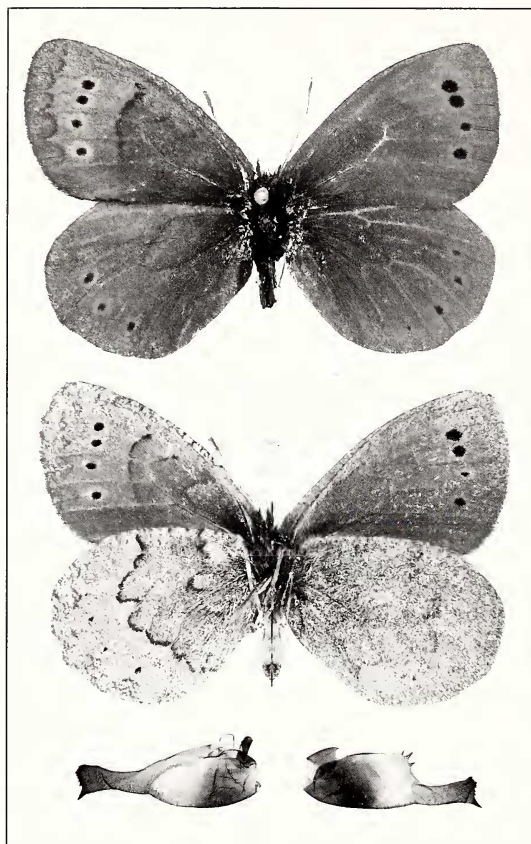


Fig. 1. Typical upperside, underside and valve of *pandrose* (left) and *sthennyo* (right).

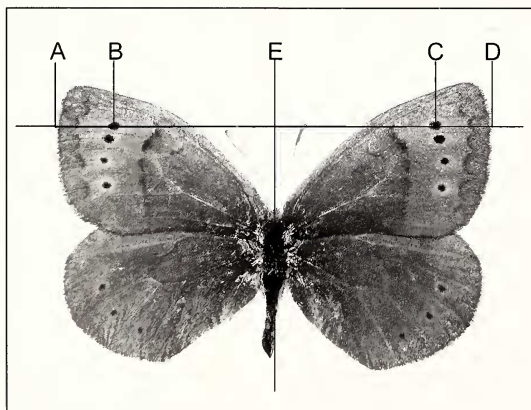


Fig. 2. Ocelli position. The ratio AB/AE was calculated from the measured AD and BC .

tribution (De Lattin 1967; Kostrowicki 1969). Arctic-alpine disjunction and Eurasian distribution are strongly correlated (Varga 1996), as both result from tundra dispersion during glacial periods. In addition, populations inhabiting the southern mountain ranges could survive in spatially restricted peripheral refugia. These were characterised by the vertical distance between the ice-surface and the snowline being sufficient to enable permanent settlement of alpine organisms in between. Through the pioneering work of Penck & Bruckner (1909, first published in separate issues 1901–1908) detailed data on glacier altitude and snowline altitude on the outskirts of the Alpine ice sheet became available for the first time. Soon, locations of potential refugia were reconstructed, and distributional areas of alpine plant species were related to them (Chodat & Pampanini 1902; Briquet 1906; Brockmann-Jerosch & Brockmann-Jerosch 1926). Meanwhile, the location of those potential refugia has been refined (Stehlik 2000; Schönschwetter et al. 2005), and postglacial dispersal routes in the Alps have been reconstructed for a considerable number of plants (Stehlik 2003, Tribsch & Schönschwetter 2003) and a few alpine animal taxa. In the latter, such reconstructions have been based on molecular markers (e.g., Schmitt & Hewitt 2004, Vila et al. 2005, Schmitt et al. 2006) or morphological characters (Holdhaus 1954, Cupedo 2004).

This paper deals with the *Erebia pandrose-sthennyo* complex, which consists of two, closely related taxa, *pandrose* (Borkhausen, 1788) and *sthennyo*

(Graslin, 1850). Because of strong morphological similarities they are widely considered conspecific (Warren 1936, Manley & Allcard 1970, Gómez Bustillo 1974, Higgins 1975, Leraut 1980). Because of certain constant differences, however, both in genital

characters and in wing design, some authors consider them specifically distinct (Willien 1990, Kudrna 1986, Lafranchis 2000). Biological evidence for either of these views is lacking.

Erebia pandrose is a tundra and high mountain species with a Eurosiberian distribution (Warren 1936, Kostrowicki 1969). The European part of the area is oreo-tundra disjunct. The tundra component includes Scandinavia and the adjacent Russia, as far as the Kanin peninsula (Warren 1936) and Kolguev Island (Tatarinov & Dolgin 1999). The oreo area is fragmented: it comprises the Alps, Pyrenees, Apennines, Carpathians, and the Balkan mountains. The Asian subarea is exclusively oreo, and is confined to the Altai-Sayan mountain range. The species is absent from the East Palaearctic tundra. Records from the Caucasus (Kostrowicki 1969) have not been confirmed and are supposedly erroneous (Nekrutenko 1990, Tuzov et al. 1997). *Erebia sthenno* has only been recorded from the central Pyrenees, where it lives in close proximity to *Erebia pandrose* (De Lesse 1952).

In the 1990's, however, the author found several populations in the southern Alps that, according to both male genital characters and wing design, belong to *sthenno*. They probably remained unnoticed because since Warren (1936) genital characters of alpine *pandrose* populations never received serious attention, as these were a priori considered not to belong to *sthenno* (Verity 1953, Varga 1971, Roos & Arnscheid 1976). As a result our actual knowledge of the geographical distribution of typical *pandrose* and typical *sthenno* characters is incomplete. This paper presents the results of a re-examination of a large number of populations, covering the whole geographical range of the *E. pandrose-sthenno* complex, and based on a predefined set of differentiating morphological characters. It aims to establish the actual geographical distribution of typical *pandrose* and typical *sthenno* characters, in order (i) to determine the validity of the taxa *pandrose* and *sthenno*, (ii) to examine to what extent their Pleistocene history can be reconstructed, based on distributional data, and (iii) to work out the taxonomic and nomenclatural implications of the results.

Abbreviations

ZMAN = Zoological Museum Amsterdam (NL); MNHL = Nationaal Natuurhistorisch Museum Leiden (NL); CFC = Collection Frans Cupedo, Geulle (NL); CSC = Collection Sergei Churkin, Moscow (RU); SP = Number of spines per valve; OP = Ocelli Position; FWD = Forewing Design; HWD = Hindwing Design; MIS = Marine Isotope Stage.

Material and Methods

Samples were studied from 43 localities. See table 1 and figure 3. (Tables in the appendix). Five differentiating *sthenno* characters have been quantified and measured as follows (figure 1; see also note 1):

Male valve: the *sthenno* male has prominent spines on the dorsal edge of the valve, which are lacking in *pandrose*.

The number of spines on the dorsal ridge of the valve (SP) was counted. Asymmetry being rule rather than exception, left and right valve were scored separately. (Stereomicroscope, 20×)

Male forewing upperside: in *sthennyo* the apical ocelli are situated closer to the wing margin than in *pandrose*.

Well set males were photographed and printed on a 2:1 scale. The position of the apical ocelli relative to the wing margin (OP) was expressed in the ratio AB/AE in Figure 2.

Male forewing upperside: in *sthennyo*, the postdiscal band is poorly developed, its edges are suffused, and the fine submarginal zigzag line, common in *pandrose*, is missing.

The development of the postdiscal field was quantified as follows:

- 0 = Band completely obscure, in ground colour.
- 1 = Lighter rings around ocelli.
- 2 = Lighter colour more extended than merely rings; less than 3.
- 3 = Lighter colour filling the postdiscal band completely, at least in cells 4 and 5, eventually in cell 3.
- 4 = Idem, including cell 2.

Distal edge of the postdiscal band:

- 0 = fading into submarginal field; 1 = distinct.

Denticulate transverse line separating submarginal and postdiscal band:

- 0 = absent; 1 = present.

The sum of the three scores is used as a measure for forewing upperside design (FWD).

Male hindwing underside: In *sthennyo* the design of the hindwing underside is poorly developed, and marginal elements (chevrons and its dark filling) are lacking.

Transverse lines.

- 0 = absent; 1 = faintly indicated; 2 = present

Ocelli.

- 0 = absent; 1 = one point in cell 2; 2 = more than one point

Chevrons.

- 0 = absent; 1 = indicated; 2 = present

The dark filling of the chevrons.

- 0 = absent; 1 = indicated; 2 = present

The sum of the four scores is used as a measure for hindwing underside design (HWD).

Female genitalia. In *sthennyo* the antevaginal plate is wider than in *pandrose*. The width of the antevaginal plate was measured. (Measuring microscope, 30×)

Deviations from normality were calculated using the Kolmogorov-Smirnov test with Lilliefors correction. For cluster analysis three algorithms were applied: Ward-method, average linkage within groups and average linkage between groups. Z-scores were standardized and squared Euclidian distance was measured. Homogeneity of variances was determined with Levene's test, and analysis of variance was performed with one-way ANOVA or through the non parametric Kruskal-Wallis test. All statistical tests

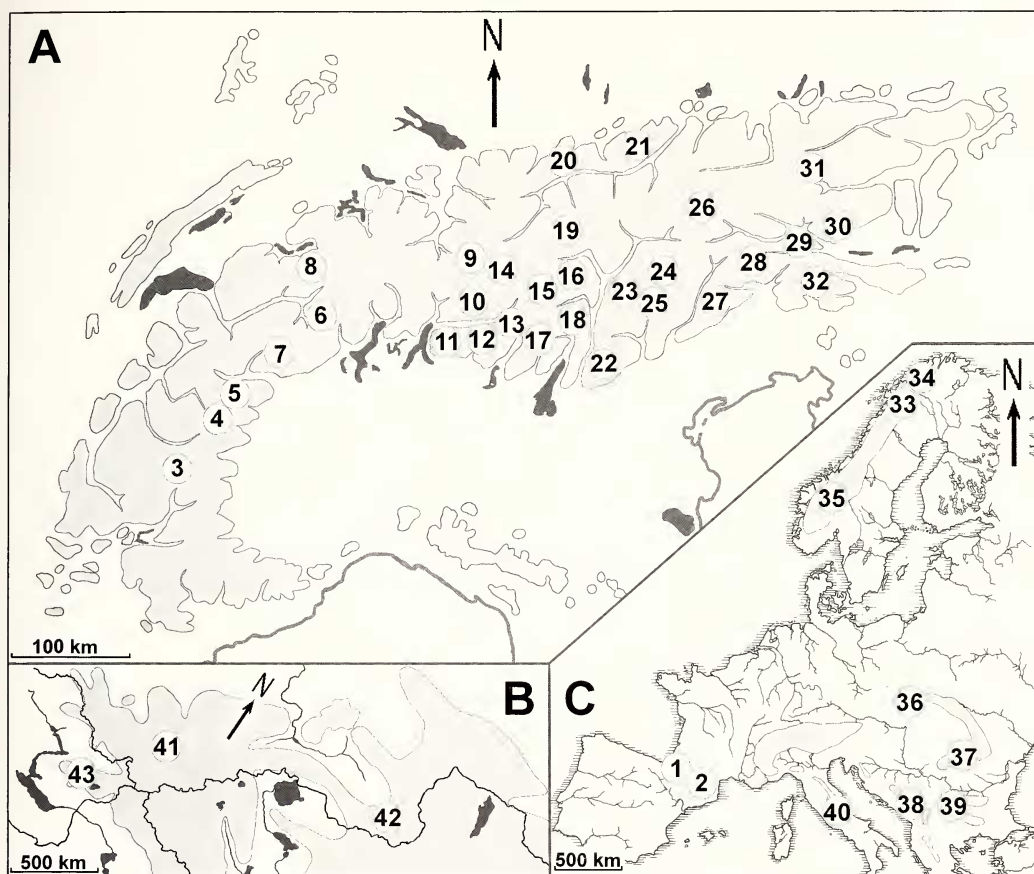


Fig. 3. Sampling sites. **A.** The Alps. Light grey = mountains >1000 m. Dark grey = lakes and coastline. **B.** Altai-Sayan. Light grey = mountains >1500 m. Dark grey = lakes and rivers. Black = political boundaries between Kazakhstan (W), Russia (N), Mongolia (E) and China (S). **C.** Europe. Light grey = main mountain systems. The numbers refer to Tab. 1.

were performed with the software SPSS 12.0. Pleistocene timetable is based on oxygen isotope dating (MIS stages).

Results and conclusions

1.1. Male characters (Fig. 4)

The population average values for each of the four variables are listed in Table 2 and graphically presented on Figure 4. Only the distribution of the number of spines per valve deviates significantly from normality (Kolmogorov-Smirnov $p < 0.001$). It is even discontinuous, with values either < 0.5 or > 1.0 . Hierarchical cluster analysis (Ward method), based on the four male characters, resulted in the dendrogram in Figure 5. The two main clusters were designated A and B. For forewing design and hindwing design (equal variances, Levene's $p = 0.445$ and 0.421 respectively) ANOVA gave a very good discrimination between the clusters A and B ($F = 15.4$ and 23.5 respectively; $p < 0.001$).

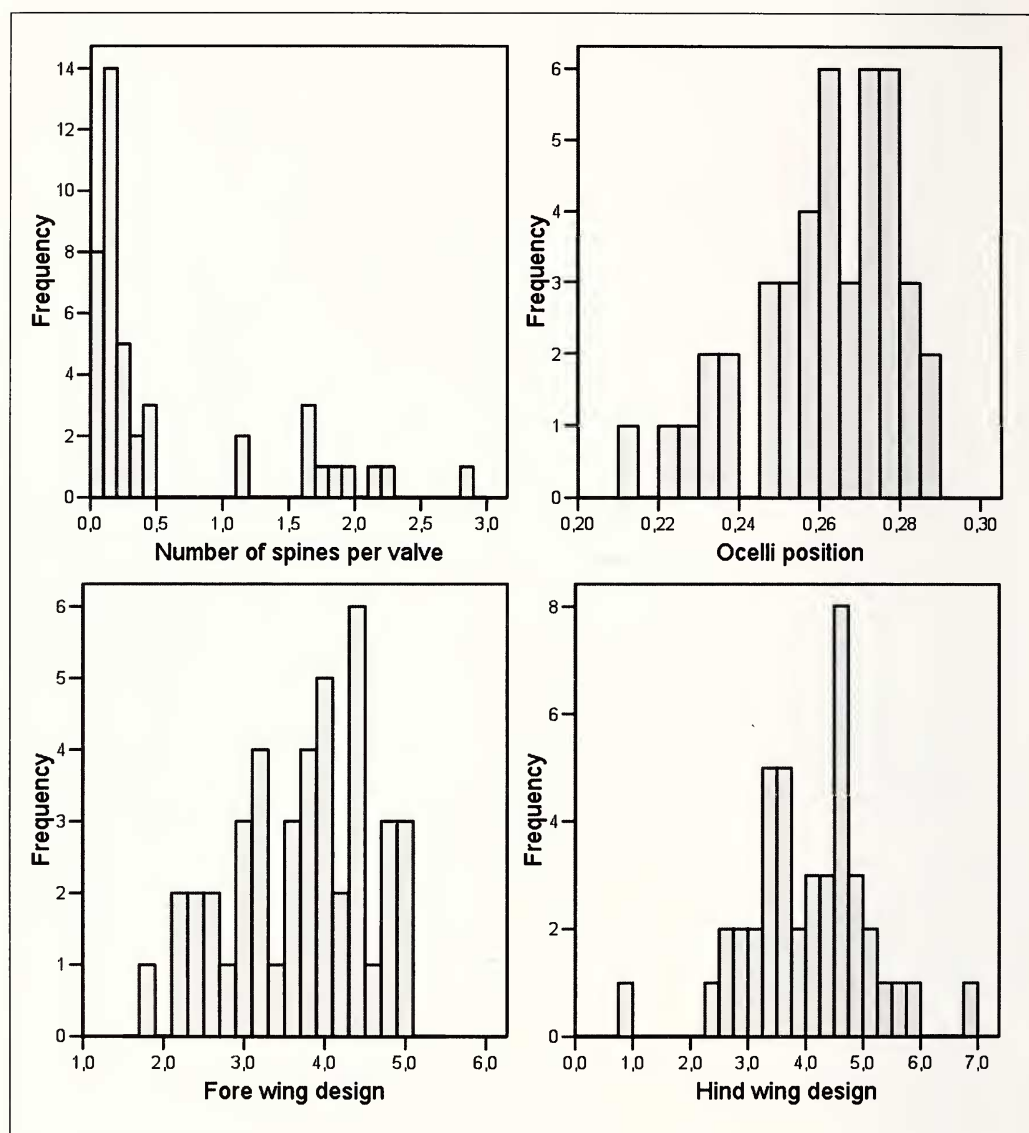


Fig. 4. Frequency distribution of the population means of the four differentiating characters in males.

in both cases). For the number of spines and ocelli position (variances significantly unequal, Levene's $p < 0.001$ and $= 0.019$, respectively) Kruskal-Wallis test confirmed significant difference between both clusters ($p < 0.001$ for both variables). Average linkage within groups resulted in identical clustering. Using between-groups algorithm, sample 33 was transferred to the B-cluster.

The main conclusion is that, on the basis of the morphological characters that are traditionally used to discriminate between *pandrose* and *sthenny*, the populations of the *E. pandrose-sthenny* complex indeed split up into two distinct groups. As the populations with typical *pandrose* characters belong to the A-cluster, and populations with *sthen-*

nyo characters to the B-cluster, these will provisionally be referred to as the *pandrose* group and the *sthenny* group, in short *pandrose* and *sthenny*, without any taxonomical bearing.

1.2. Female genitalia

There is a discrepancy between the Pyrenean *sthenny* population (sample 1) and all other populations investigated. Because of the extremely small sample size ($n=1-5$ per population), these results were omitted from the cluster analysis. If the available data were included, sample 1 would branch off from the B-cluster at a distance of 7 scale-units (not shown).

1.3. Geographical distribution

The geographical distribution of the taxon *sthenny*, hitherto considered a Pyrenean endemic, is far more extended than ever thought. It inhabits three major mountain systems and at least one small one: the Pyrenees, the southeastern Alps, the Altai, and the Durmitor in Montenegro.

Within the *pandrose* group, each of the studied characters showed a continuous variation, the extremes of which can be characterised as “typical *pandrose*” and “more or less *sthenny*-like” respectively. To what degree each of the populations of the *pandrose* group tends towards a *sthenny* habitus is best visualised by a simple ranking (Table 3), based on the rescaled (0–100) sum of the rescaled scores for the four characters. The most typical *pandrose* (sum = 0) ranks at the top. Geographical distribution in relation to ranking was not random. In Figure 6, populations with a sum ≤ 50 and those with a sum > 50 are plotted in different symbols. The most *sthenny*-like populations turned out to be concentrated in the eastern Alps, in a zone bordering the area of the *sthenny* group. Beyond the Alps such populations were found in Scandinavia only. The other extreme, the most typical *pandrose* populations, were found in the southern Carpathians and the Balkans (Bucegi and Rila), followed by the Siberian populations (Altai and Sayan).

Discussion

1. Monophyly of the *pandrose* group and the *sthenny* group

The *pandrose* group and the *sthenny* group share three mountain systems: Pyrenees, Alps, and Altai. It is quite unlikely that the morphological differences between both groups arose independently in each of these regions. Obviously, *pandrose* and *sthenny* form two monophyletic groups, i.e. the differences between them must date back to their respective common ancestors. The primary dichotomy in the dendrogram thus reflects the oldest detectable geographical disjunction within the *Erebia pandrose-sthenny* complex, which has resulted in two isolated populations that subsequently differentiated into the *pandrose* ancestor and the *sthenny* ancestor.

The fact that the most *sthenny*-like populations in the Alps are concentrated in a zone bordering the area of the *sthenny* group, strongly suggests that they originate from

postglacial intermingling in a contact zone. Apparently, *pandrose* and *sthenny* did interbreed where they met. That was emphatically the case in the eastern Alps. To a minor extent, however, intermingling with *sthenny* genes has taken place anywhere in the Alps: populations with a relatively high score for one of the studied characters are found throughout the Alps, and in the Apennines (Table 3).

2. Pleistocene history

2.1. Würm–glacial refuges in the Alps, the Apennines, the Carpathians, and the Balkans

Each population of the *sthenny* group, and some populations of the *pandrose* group, can easily be related to one of the well known glacial refugia. For the remaining *pandrose* populations, there is a logical relation with a refugium, but they cannot be morphologically linked to it, as this study focuses merely on differentiating characters between *pandrose* and *sthenny*. Those refugia are printed in small font.

The Bergamasque Alps

The Bergamasque Alps remained largely unglaciated during the Würm glaciation (MIS2-4, 75–10 ky BP). They harboured an isolated refugial flora and fauna, including *sthenny*. During Würm, the valleys of Adda and Oglio attained their actual depth by glacial erosion, which largely prevented post-glacial expansion. *Sthenny* could just infiltrate the southern Ortler group across the Aprica pass, which accounts for the intermediate population found there (sample 15, see table 3). The Bergamasque *sthenny* populations show endemic differentiations (see the taxonomy and nomenclature section).

The Brescian refugium

The area between Lake Iseo and Lake Garda is considered here a separate refugium, called Brescian refugium. From this refuge the Adamello-Presanella group has been repopulated in postglacial times. It has been noticed for a long time that the populations of the Adamello-Presanella group and those of the adjacent Brenta group are strikingly different (Hartig 1937). That is confirmed by the results of this study: the former has a *pandrose* habitus, the latter a prominent *sthenny* habitus (sum = 49 and 91 respectively). This applies also to the southernmost known population in the Adamello group, on the Passo Croce Domini, which contributed substantially to sample 17. Thus, it cannot be excluded that a population with a *pandrose* habitus has survived the Würm-glacial in the Brescian refugium, whereas the adjacent refugia were inhabited by *sthenny*. In addition, postglacial gene flow across the Passo Carlomagno must have been minimal or absent, a phenomenon that has also been reported for *Erebia pluto* (Cupedo 2004).

The refugia east of Lake Garda

The southern-alpine *sthenny* populations East of Lake Garda have their origin in a series of well known small refuges on the southern border of the eastern Alps (Tribsch & Schönswetter 2003): the Lessinic Alps, the Venetian and Carnic Pre-Alps, and the

Julian Alps. Postglacially they just moved to higher altitudes, and spread more or less northwards, into the Dolomites and the mountains south of the High Tauern watershed, where they apparently intermingled with populations of the *pandrose* group. The populations of the Lessinic Alps and the Venetian Pre-Alps (samples 22 and 27) have been living, up to present time, in unglaciated areas.

The East-alpine refugium

The vast refugial area that existed in the non-glaciated parts of the Styrian Alps (Penck & Bruckner 1909, Tribsch & Schönschwetter 2003) was another dispersion centre of the *pandrose* group. Populations on the Zirbitzkogel (Reichl 1992) and in the eastern Karawank mountains (Jakšić 1998) have even persisted here within the refugial area to date. At least the populations of Gurktal Alps and Niedere Tauern (samples 29, 30, 31) must have their origins in this refugium.

The Apennines

During glacial stages the Apennines were ecologically contiguous with the Ligurian and Maritime Alps, and must have acted as an important refugium for many species. This is reflected in the morphological resemblance of their *Erebia* species with western Alpine forms. For *E. cassioides* this relation has been confirmed by molecular data (Lattes et al. 1994). The small witness population in the Laga mountains proves that also *pandrose* withdrew into the Italian peninsula. As there is only one pathway, there is no doubt that the Apennines were colonised from the western Alps. (Note that this does not necessarily imply a postglacial colonisation of the western Alps from the Apennines!)

Northern refugia

The northern limestone Alps must logically be colonised from refuges at its northern outskirts, or even from the periglacial tundra.

Western alpine refugia

Vast refugia existed in the French Pre-Alps (Vercors, Diois, Provence), many narrow refugial areas were found at the eastern slopes of the Cottian and Graian Alps (Briquet 1906). Undoubtedly these refugia contributed to the present-day *pandrose* populations in the western Alps, but this cannot be inferred from the present study.

Carpathians and Balkans

Varga (1975b) demonstrated that populations of many species in the Bulgarian mountains (Stara Planina, Rila, Pirin), including *Erebia pandrose*, were morphologically closely related to Carpathian populations. He made clear that the Balkan mountains were colonised from the southern Carpathians, and that the oldest differentiations among Balkan *Erebia* dated to the Würm-glacial. The present data (samples 37 and 39) agree with that hypothesis. In the western Balkans on the other hand, the Dinarics and the mountains of Bosnia-Herzegovina, Montenegro, and Macedonia were connected with the Julian Alps, which harbour closely related butterfly faunas (Varga 1975b). The fact that the Julian Alps and the Durmitor currently are both inhabited by *sthenny* supports such a connection.

2.2. Pre-Würm history

Dispersion routes. Both the *pandrose* group and the *sthennyo* group show distribution patterns that range from the European mountains to Central Asia. This is due to the fact that dispersion of both groups took place along the same pathway: the glacial trans-palaeartic tundra belt (De Lattin 1967, Kostrowicki 1969). As, however, *pandrose* and *sthennyo* would have intermingled wherever they met, they can not have occupied the tundra belt simultaneously. Consequently, *pandrose* and *sthennyo* must have spread in two waves, at different moments in history, i.e. during different glacial cycles.

Sequence. The populations of the *pandrose* group are rather uniform throughout their territory. They differ merely in the extent of the *sthennyo* influence. The *sthennyo* populations are morphologically far more differentiated: the Kazakhstan population shows a different arrangement of forewing ocelli and a different forewing shape; the Pyrenean population developed an apomorphic genital character in the females; the populations of the Bergamasque Alps differ in their wing design from the remaining populations in the south-alpine subarea (see the taxonomy and nomenclature section). That suggests that spread and subsequent disjunction of the *pandrose* group is of more recent date than that of the *sthennyo* group. This is confirmed by their actual distribution in the Alps: *pandrose* is widespread in the northern regions, bordering the glacial tundra belt along which both groups have reached the Alps, whereas *sthennyo* has been completely cut off from the previous tundra zone: it has been forced into refugial areas, “dead ends”, on the southern outskirts of the Alps.

Dating. The witness population in the Apennines unequivocally proves that the *pandrose* group was present in the Alps before the beginning of the Würm glacial, i.e. during the Riss-Würm interglacial (MIS5, 128-75 ky BP). The same goes for the southern Carpathians, in view of the presence of *pandrose* in the Rila mountains. Thus, the spread of *pandrose* in the tundra belt has to be dated at its latest to the Riss glaciation (MIS6, 185-128 ky BP) [Note 2+3]. Consequently, the spread of *sthennyo* along the tundra belt took place at its latest during the Mindel glaciation (MIS8, 300-242 ky BP). That means that more or less unmixed *sthennyo* populations persisted in the southeastern Alps for at least two glacial cycles. This is probably due to the predominant east-west orientation of mountain chains in this part of the Alps. In the western Alps, however, no geographic barrier prevented intensive gene flow between *pandrose* and *sthennyo*. As a result, no *sthennyo* populations exist there today, but a number of *pandrose* populations show *sthennyo* traits to some degree (cf. the mean SP values of samples 4 and 7, table 3).

Scandinavia. The Scandinavian populations must result from the same two colonisation waves. During Riss, however, Scandinavian *sthennyo* populations were shoved south by the growing land ice cap and survived at its edge. Here they intermingled with *pandrose* already during glacial time, prior to the repopulation of Scandinavia. As a result Scandinavia nowadays is inhabited entirely by intermediate populations, in contrast with the Alps, where postglacial encounter led only to borderline mixing. Nonetheless, the Scandinavian populations are far from uniform, as was already stated by Henriksen & Kreutzer (1982). Therefore, it is not surprising that one of these populations (sample 33) is placed in the *sthennyo* cluster when using a different algorithm for hierarchical cluster analysis.

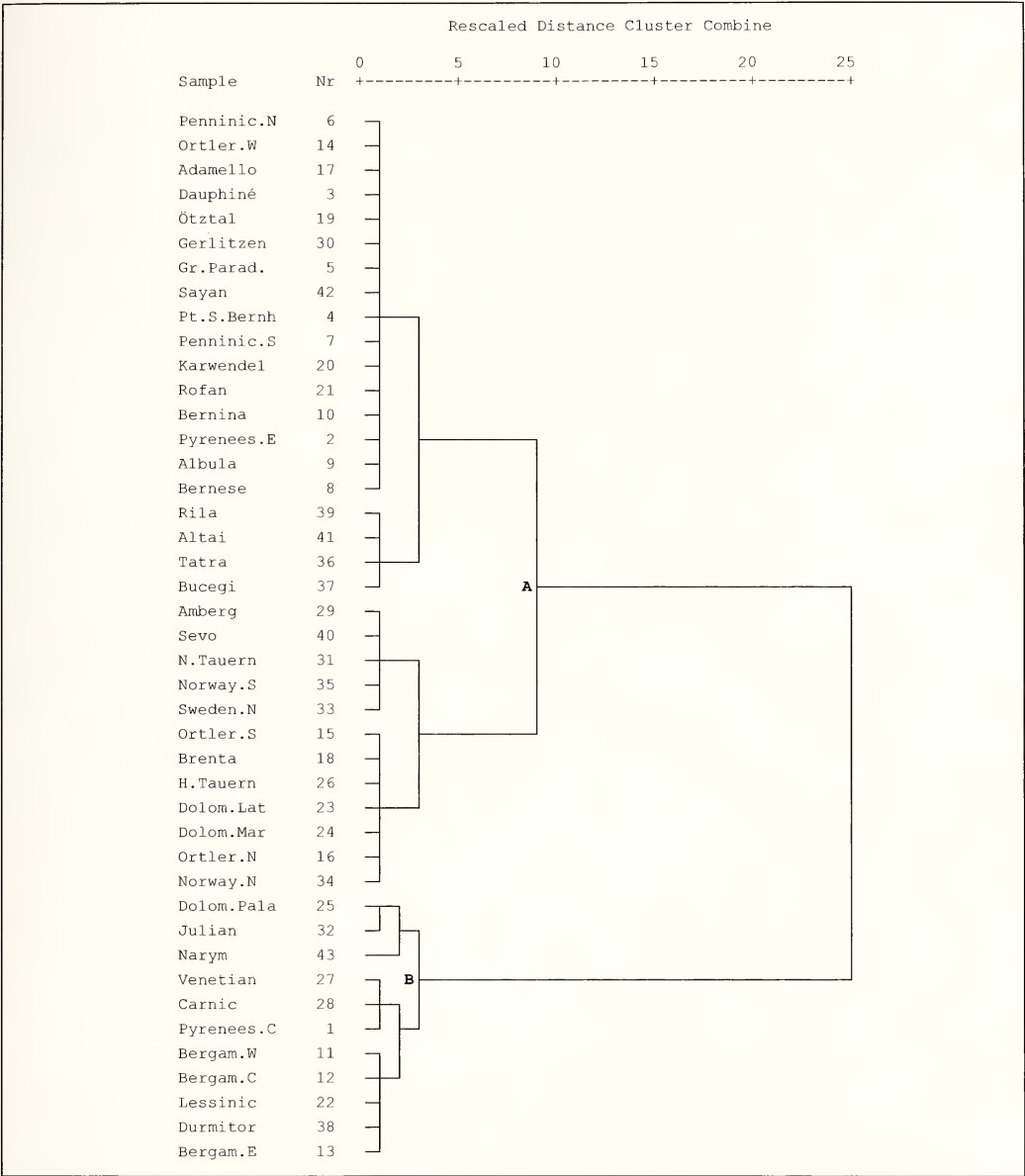


Fig. 5. Dendrogram resulting from hierarchical cluster analysis (Ward algorithm).

Centres of differentiation. The results of this study provide no clue to the geographic differentiation centres of the ancestors of the *pandrose* group and the *sthenny* group, nor to the direction of their glacial expansion. From the above can only be inferred that, prior to the dispersion of *pandrose*, *sthenny* already occupied the European mountains (Alps and Pyrenees), the European tundra (Scandinavia), and the Siberian mountains (Altai). That leaves the Siberian tundra as a hypothetical centre of origin for *pandrose*. The differentiation of *pandrose* and *sthenny* might, theoretically, have resulted from an early Pleistocene oreo-tundral disjunction in the eastern Palaeartic.

3. Taxonomy and nomenclature

3.1. The type locality of *Erebia pandrose* Borkhausen, 1788

Erebia pandrose was originally described as *Papilio castor* Esper, 1781. Borkhausen (1788) replaced this name (a primary homonym of *Papilio castor* Cramer, 1775) by *pandrose*. Description and type locality, however, were fixed by Esper. His material came from “Steiermark” (Stiria), without further specification. The only Stirian massifs harbouring *E. pandrose* are the Niedere Tauern and the northern Saualpe (Reichl 1992). In the material investigated for this study, sample 31, from the western end of the Niedere Tauern, is regarded to be closest to nomotypical *Erebia pandrose*.

3.2. The taxonomic status of the *sthenny* group

In the Pyrenees, despite intensive and targeted research by de Lesse (1952), *sthenny* and *pandrose* were nowhere found living sympatrically. He just found one possible hybrid, flying together with some *pandrose*, in the region separating the areas of *sthenny* and *pandrose*. His observation has been interpreted as a sympatric occurrence (Lafranchis 2000), but is certainly not a proof of reproductional isolation. In the Alps, both groups have intermingled where they met. That implies that, at least in the Alps, no reproductive barriers exist between members of the *pandrose* group and members of the *sthenny* group. Consequently, *pandrose* and *sthenny* are to be considered conspecific.

Nonetheless, there are constant anatomical differences between unmixed populations of the two groups, which result, as has been shown, from at least 240,000 year of isolation. The subspecies of *Erebia pandrose* thus can be grouped in two monophyletic aggregates of subspecies which, according to Art. 6.2 of the Code, should be designated as *Erebia pandrose* (group *pandrose*) and *Erebia pandrose* (group *sthenny*) (ICZN 2000).

3.3. *Erebia pandrose pandrose* Borkhausen, 1788 and *E. pandrose ingana* Fruhstorfer, 1911

In the Alps, two subspecies of the *pandrose* group have been described. The validity of ssp. *ingana*, characterised by the intensively coloured postdiscal band and the prominent black spots on the forewing upperside, has long been questioned. Warren (1936) states that “such specimens occur wherever *pandrose* flies, and always in company with poorly marked specimens”. Von der Goltz (1938), after studying Fruhstorfer’s cotypes, concluded that the typical characters of *ingana* are individual characteristics, not typical of the population. Both Warren’s and Von der Goltz’s opinion are confirmed by the large sample 5, which was collected at exactly the same place where Fruhstorfer collected his type series. Fruhstorfer’s description applies to a minority of brilliantly coloured specimens, which occur equally in many other samples. This explains why distributional data for *ingana* of leading authors are so different, sometimes even contradictory, and lack any zoogeographical logic (compare Fruhstorfer 1911, Hartig 1937, Verity 1953, Varga 1975b, Roos & Arnscheid 1976 and Arnscheid 1981). In addition,

none of the characters investigated in this study justifies a subdivision of the alpine populations of the *pandrose* group into two morphologically defined and geographically coherent units. Consequently, *Erebia pandrose ingana* Fruhstorfer, 1911 is to be considered a subjective junior synonym of *Erebia pandrose pandrose* (Borkhausen, 1788).

3.4. *Erebia pandrose marmolata* Dannehl, 1927 and *E. pandrose infraclara* Verity, 1953

In the Alps, two subspecies of the *sthennyo* group have been described. The type locality of *marmolata*, in spite of its name, is the Pala group (Dannehl, 1927 p. 3), the type locality of ssp. *infraclara* is Val Milbach above Sappada in the Carnic Pre-Alps (Verity 1953, p. 132). Samples 25 and 28 have been collected at both type localities. Valve morphology and wing design are strikingly similar. Indeed, Dannehl's description of the *marmolata* upperside is an accurate description of the *sthennyo* form inhabiting the southern Alps from the Adige valley to the Tagliamento valley, including Verity's *infraclara*. According to Warren (1936) the ground colour of the hindwing underside is the main differentiating character. In both sample 25 and 28, however, fresh males have the silvery grey hindwing underside which Verity considered typical of *infraclara*, whereas in worn males the ground colour has turned into a rusty grey-brown, fitting Dannehl's description of *marmolata*. The only real difference is found in the sprinkling of dark scales on the hindwing underside, which is denser in Pala specimens than in Sappada specimens. Before describing *infraclara* (1953), Verity explicitly denied the subspecific nature of *marmolata*, stating that each of the *marmolata* characters mentioned by Dannehl, is found in other regions as well. As was shown earlier in this paper, this is correct: *sthennyo* characters do occur in many alpine populations. In fact, Verity misled himself by taking the description of *marmolata* as a reference, instead of material from the type locality. Had Verity's collection contained specimens from the Pala group, ssp. *infraclara* would not have been described. Consequently, *Erebia pandrose infraclara* Verity, 1953 is to be considered a subjective junior synonym of *Erebia pandrose marmolata* Dannehl, 1927.

The currently known range of ssp. *marmolata* covers the Bergamasque Alps, the Lessinic Alps, the Venetian Pre-Alps, the adjacent Pala group, the Carnic Pre-Alps, the Julian Alps, and the Durmitor. As to the Monte Baldo: photographs of the (poor) existing material (Sala 1996, Sala pers. com.) suggest that the population belongs to the *sthennyo* group. However, this could not be confirmed by genital examination, as no material was available for dissection. The populations inhabiting the northern and western Dolomites, the Brenta group, and Eastern Tyrol are morphologically intermediate between *marmolata* and *pandrose*.

3.5. Geographical variation within ssp. *marmolata* (Fig. 7)

In the Bergamasque Alps 27% of the individuals have only the two apical spots on the forewing upperside. In all other investigated samples this feature was encountered only incidentally. In the Julian Alps the forewing design is extremely variable, which is typi-

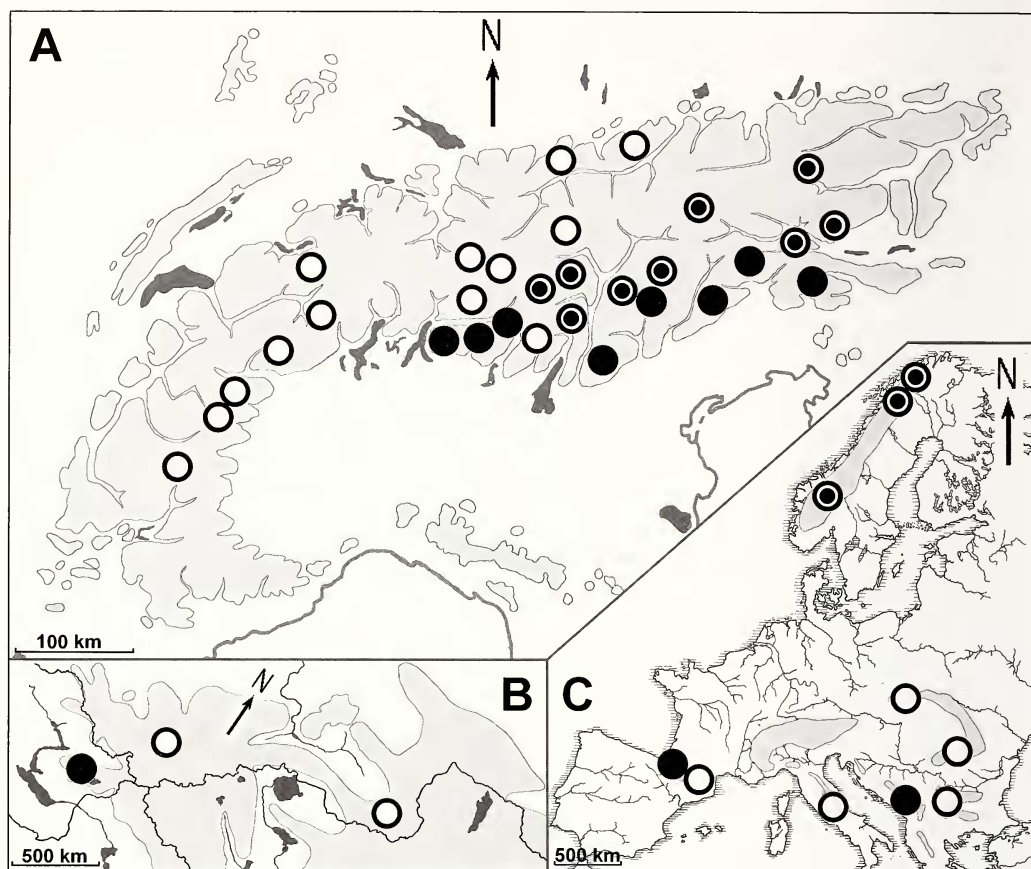


Fig. 6. Geographical distribution of the populations of the *sthenny* group (black) and the *pandrose* group, the latter in relation to their ranking in table 3. Open circle: sum ≤ 50 ; Circle with black centre: sum > 50 .

cal of populations of a mixed origin. The observed variation might be due to intermingling with *pandrose* from the Karawank mountains, which, however, is not supported by a lower SP value.

3.6. The Asian populations of the *sthenny* group

Asian populations of *Erebia pandrose* have been described as ssp. *orientalis* Goltz, 1930. This name, a junior homonym of *Erebia epiphron orientalis* Elwes, 1900, was replaced by *yernikensis* Korshunov, 1995 (Korshunov & Gorbunov 1995). Both the type locality (Sayan mountains) and the excellent description unmistakably apply to representatives of the *pandrose* group, represented in this study by samples 41 and 42. The population of the *sthenny* group inhabiting the Kazakhstan part of southern Altai (sample 43), has not been described yet. It differs from the other known populations of the *sthenny* group by its elongate forewing shape, and by the forewing ocelli being positioned as in the *pandrose* group (Figure 8). It is described here as a new subspecies within the *sthenny* group.

Erebia pandrose (sthenny) narymica ssp. n.

(Figs 8, A1–B8)

Material. Holotype: ♂, label in Cyrillic script (figure 9), transliteration: 'V[ostochno]-Kaz[akstanskaya] obl[ast'] Bolschenar.[ymskiy] r[ayo]n l s[elo] Novoberezovka 2800 [m] A.G.Aniskovich l 24.VI 1986', CFC. – Paratypes: 1♂, label in Cyrillic (figure 9), transliteration: 'S.[elo] Novoberezovka 3000 m. l Bolshenarymskiy r-[ayo]n l Vostochno-Kazakst.[anskaya] obl.[ast'] E. pandrose 2.7.1986.', CFC; 1♂ 'E. Kazakhstan l South Altai l Narymsky range l Novoberezovka v. l2800 m. l25-26.06.1986 l A. Aniskovich leg.', CFC; 1♂, 1♀ '3-7-1986 USSR l Vostočno-Kazachst. l S. Novoberjezovka l 3000 m leg. Anisković', ZMAN; 1♂, label in Cyrillic script, transliteration: 'V-Kaz obl Bolschenar. rn l s. Novoberezovka 2800 l A.G.Aniskovich l 30.VI 1986', CSC.; 2♂, label in Cyrillic script, transliteration: 'V-Kaz obl Bolschenar. rn l s. Novoberezovka 2800 l A.G.Aniskovich l 2.VII 1986', CSC.; 4♂, 1♀, 'E. Kazakhstan l South Altai l Narymsky range l Novoberezovka v. l2800 m. l25-26.06.1986 l A. Aniskovich leg.', CSC.

Holotype and paratypes form a series collected by A. Aniskovich & G. Makhat on a trip in the Narymsky Range from 24 June until 3 July 1986. The specimens were papered and dispersed among several collectors, who wrote their own labels, according to Aniskovich's data. The holotype and three paratypes bear handwritten labels by Aniskovich.

Description. Male forewing length: 21–23 mm. Forewing with pointed apex; upper-side pattern indistinct, submarginal zigzag line absent; position of forewing ocelli as in *Erebia p. pandrose*, not shifted towards the wing margin as in *Erebia p. sthenny*. Hindwing underside design vague, ocelli and marginal elements absent.

Male genitalia: Dorsal ridge of valve provided with a prominent spines, with mean of 2.8 spines per valve in studied sample.

Diagnosis. Differs from all subspecies of the *Erebia pandrose (pandrose)* group by the spines on the valve and the indistinct pattern of the forewing upperside and the hindwing underside. Differs from all other subspecies of the *Erebia pandrose (sthenny)* group by the pointed forewing, and by the forewing ocelli being situated less close to the wing margin.

Etymology. The name refers to the type locality, the Narym mountains (Narymsky Range).

Geographical distribution. Apart from the type locality (South Altai, Narym Mountains in East Kazakhstan, Bolshenarymskoye district, south-east of the city of Novoberezovka), the new ssp. is known from the adjacent Sarym-Sakty mountains (CSC).

Remark. Males from the Lystviaga and Kholsun mountains (Russian Altai) have similar valves, but the wing design tends towards *yernikensis* (V. Lukhtanov, pers. comm.). Probably intermediate populations exist.

4. Checklist

4.1. *Erebia pandrose (group pandrose)*

Diagnosis: mean number of spines per valve < 0.5. Design of forewing upperside and hindwing underside complete and distinct.

• *Erebia pandrose (pandrose) pandrose* (Borkhausen, 1788).

(=*Erebia pandrose (pandrose) ingana* Fruhstorfer, 1911, **syn. n.**)

Distribution: Alps. Absent from the area of the *sthenny* group in the south-east (see below), and from the Chartreuse and the Vercors in the west (Willien 1990).



Fig. 7. European representatives of the *sthenno* group of *E. pandrose*. **A.** *ssp. sthenno*, Central Pyrenees (sample 1). **B.** *ssp. marmolata*, Bergamasque Alps (sample 11–13). **C.** *ssp. marmolata*, Pala group (sample 25). **D.** *ssp. marmolata*, Julian Alps (sample 32). **E.** *ssp. marmolata*, Durmitor (sample 38).



Fig. 8. *Erebia pandrose* (*sthennyio*) *narymica* ssp. n., (A=upperside, B=underside) and *Erebia pandrose* (*pandrose*) *yernikensis* Korshunov, 1995, (C=upperside, D=underside). Row 1-7: males; row 8: females. A1 and B1: holotype, A2 – B8 paratypes.

Note: Most populations are in variable degree intermediate between the *pandrose* group and the *sthenny* group. This is most prominent in the eastern Alps.

- *Erebia pandrose* (*pandrose*) *sevoensis* Willien, 1975.
Distribution: Apennines. One single population on the Pizzo di Sevo in the Monti della Laga, Lazio (Chiavetta 2000).
- *Erebia pandrose* (*pandrose*) *yernikensis* Korshunov, 1995.
Distribution: Altai and Sayan Mountains (Siberia), recently also found in the Barguzin Mountains in Transbaikalia (S. Churkin, pers. comm.).
- *Erebia pandrose* (*pandrose*) *gracilis* v.d. Goltz, 1930.
Distribution: Pyrenees. Occupies a restricted region in the French provinces of Arriège and Pyrénées Orientales, in the Spanish provinces of Lleida and Girona, and in Andorra (Gómez Bustillo & Fernández-Rubio 1974, Willien 1990).
- *Erebia pandrose* (*pandrose*) *roberti* Peschke, 1920.
Distribution: northwestern Carpathians. Found in the High Tatra, Lower Tatra, Belér Alps and Liptau Mountains (Moucha 1959, Krzywicki 1966, 1982).
- *Erebia pandrose* (*pandrose*) *cibiniaca* Dannehl, 1927
Distribution: eastern and southern Carpathians. Found in the Bihar, Retezat, Cibin, Bucegi, and Rodna Mountains (Hormuzaki 1901, Varga 1971).
- *Erebia pandrose* (*pandrose*) *ambicolorata* Varga, 1971.
Distribution: Rila mountains (Varga 1971).
Note: Subspecies *roberti*, *cibiniaca*, and *ambicolorata* are closely related. They share the pronounced design, especially of the marginal elements, on the hindwing underside. The differences have been worked out by Varga (1971).
- *Erebia pandrose* (*pandrose*) *lappona* Thunberg, 1791.
Distribution: Scandinavia, Kanin peninsula and Kolguev Island (Warren 1936, Tatarinov & Dolgin 1999).
Note: A rather heterogeneous group of populations that are morphologically intermediate between the *pandrose* group and the *sthenny* group. They are provisionally placed within the *pandrose* group.

4.2. *Erebia pandrose* (group *sthenny*)

Diagnosis: the mean number of spines per valve >1. Design of forewing upperside and hindwing underside incomplete and more or less suffused.

- *Erebia pandrose* (*sthenny*) *sthenny* (Graslin, 1850).
Distribution: Pyrenees. Confined to the French departments of Pyrénées Atlantiques, Hautes Pyrénées, Haute Garonne and Arriège, and the Spanish provinces of Lleida and Huesca (Gómez Bustillo & Fernández-Rubio 1974, Willien 1990).
- *Erebia pandrose* (*sthenny*) *marmolata* Dannehl, 1927.
(= *Erebia pandrose* (*sthenny*) *infraclara* Verity, 1953, **syn. n.**)

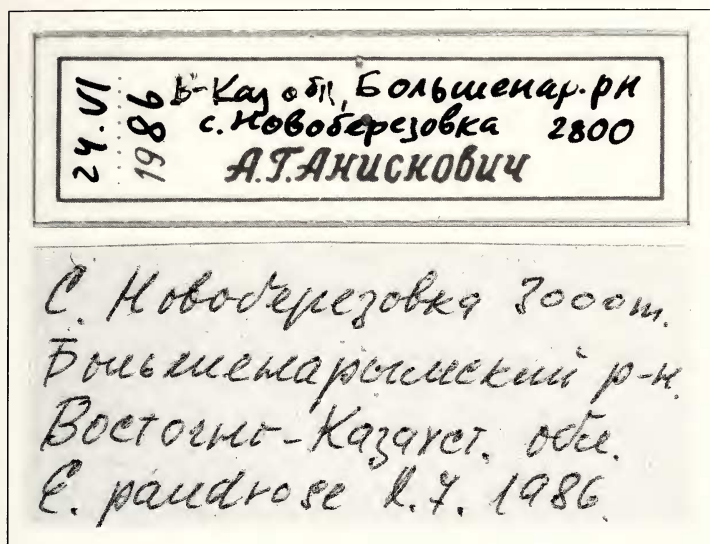


Fig. 9. *Erebia pandrose* (*sthenno*) *narymica* ssp. n., label of holotype (top) and of paratype no. 1 (bottom).

Distribution: the ssp. occupies three separated subareas.

- a. The Bergamasque Alps.
- b. The southeastern Alps, from the Lessinic Alps (possibly from Monte Baldo) to the Julian Alps, and penetrating into the Pala group of the Dolomites.
- c. The Durmitor (Montenegro). Probably all populations in Bosnia-Herzegovina, Montenegro, Macedonia (Jakšić 1988), and in Albania (Turner 1964) belong to this subspecies.

Erebia pandrose (*sthenno*) *narymica* **ssp. n.**

Distribution: Hitherto known from the Narym and Sarym-Sakty mountains in the Kazakhstan part of the Altai [Note 4].

Notes.

1. Differentiating characters between *pandrose* and *sthenno* have been taken from De Lesse (1952) and Warren (1936). De Graslin (1850), describing *Erebia sthenno*, was not even aware of the existence of *E. pandrose*. He described the species as being different from what he called *E. manto* but what, according to his description, most probably was *E. pronoe*.
2. From the present data it cannot be inferred whether *pandrose* colonised the Pyrenees already during the Riss glaciation, or reached them from the Alps during Würm.
3. As far as distributional events (expansion, or withdrawal into refuges) are being related to a glacial or interglacial period, this should be regarded a minimum dating. Glacial cycles may have passed by without recognisably affecting the overall distribution of a taxon.

4. It may well be that specimens of this subspecies have already been known to lepidopterists for a long time, possibly even from other localities. Warren (1936) writes that “in the Sayan the f. *aglauros* is the prevalent male form”, and Varga (1971) states that the Scandinavian and the Central Asiatic form are very similar, characterised by its hazy, monotonous colouring and frequent occurrence of the f. *aglauros*. Both statements are in sharp contrast with v. Goltz’ description of ssp. *orientalis* (= *yernikensis*) and with the habitus of the *yernikensis* populations investigated for this study, but do apply to *narymica*.

Acknowledgements

I am indebted to those who helped to bring together the material for this study: Mr. Sergei Churkin (Moscow, RU), Prof. Vladimir Lukhtanov (St. Petersburg, RU), Dr. Roman Yakovlev (Barnaul, RU), Dr. Oleg Kosterin (Novosibirsk, RU), Prof. Nils Ryrholm (Uppsala, S), Dr. Jostein Engdal (Saetre, N), Mr. Günther Stangelmaier (Villach, A), Mr. Adriano Teobaldelli (Sforzacosta, I), Mr. Giovanni Sala (Salò, I), Mr. Jaap Poot (Beek, NL); to the curators who gave me access to museum collections or loaned me material: Dr. Rienk de Jong (RMNH Leiden, NL), Dr. Willem Hogenes (ZMAN Amsterdam, NL), Dr. Peter Huemer (TLM “Ferdinandum” Innsbruck, A), Dr. Mihai Stănescu (NMNH “Grigora Antipa” Bukarest, RO) and Dr. Norbert Lenz (Löbbecke Museum Düsseldorf, D); to the Administration of the Gran Paradiso National Park (Torino, I) for the authorisation to collect a sample at the type locality of ssp. *ingana* within protected area. I am particularly grateful to Dr. Thomas Schmitt (Trier, D) and Dr. Marta Vila (A Coruña, E), whose comments led to substantial improvements of the manuscript.

References

- Arnscheid, W. 1981. Die Macrolepidopteren-Fauna des Sonnentäl-Nonsberggebietes (Val di Sole und Val di Non in Oberitalien) (Insecta: Lepidoptera). – Studi Trentini di Scienze Naturali **57**(1980): 95–245.
- Borkhausen, M. B. 1788. Naturgeschichte der europäischen Schmetterlinge nach systematischer Ordnung. – Varrentrapp und Wenner, Frankfurt.
- Briquet, J. 1906. Le développement des flores dans les Alpes occidentales, avec aperçu sur les Alpes en général. Pp. 130–173 – In: Wettstein, R., Wiesner, J. & A. Zahlbruckner (eds): Wissenschaftliche Ergebnisse des Internationalen Botanischen Kongresses Wien 1905. – Gustav Fischer, Jena.
- Brockmann-Jerosch, H. & M. Brockmann-Jerosch 1926. Die Geschichte der Schweizerischen Alpenflora. Pp. 1110–1215 – In: Schröter, C. (eds): Das Pflanzenleben der Alpen. – Raustein, Zürich.
- Chiavetta, M. 2000. Le farfalle d’Italia. Atlante biogeografico. – Nuovo editoriale Grasso, Bologna, 111 pp.
- Chodat, R. & R. Pampanini 1902. Sur la distribution des plantes dans les alpes austro-orientales et plus particulièrement d’un choix de plantes des alpes cadoriques et venitiennes. – Le Globe **41**: 1–40.
- Cupedo, F. 1997. Die geographische Variabilität und der taxonomische Status der *Erebia manto bubastis*-Gruppe, nebst Beschreibung einer neuen Unterart (Nymphalidae: Satyrinae). – Nota Lepidopterologica **20**: 3–22.
- Cupedo, F. 2004. Geographische Variabilität und spätglaziale Einwanderwege von *Erebia pluto* (de Prunner, 1798) in der Ortlergruppe und den Ötztaler Alpen (Nymphalidae). – Nota Lepidopterologica **26**: 137–152.
- Dannehl, F. 1927. Neue Formen und geographische Rassen aus meinen Rhopaloceren-Ausbeuten der letzten Jahren. – Mitteilungen der Münchner entomologischen Gesellschaft **17**: 1–8.
- Esper, E. J. C. 1781. Die Schmetterlinge. Erster Teil, zweiter Band. – Walthers, Erlangen.
- Fruhstorfer, H. 1911. Neue paläarktische Rhopaloceren. – Societas Entomologica **25**: 95–96.
- Goltz, [D]. H. v.d. 1930. Neue Erebiensformen. – Deutsche Entomologische Zeitschrift Iris, Dresden **44**: 78–82.
- Goltz, D. H. v.d. 1938–1939. Bemerkungen über Erebiens. – Deutsche Entomologische Zeitschrift Iris, Dresden **52**(1938): 160–171; **53**(1939): 36–48; 74–88.

- Gómez Bustillo, M. R. & F. Fernández-Rubio 1974. Mariposas de la Península Ibérica. II Ropalóceros. – Ministerio de Agricultura, Madrid. 258 pp.
- Graslin, M. A. de 1850. Notice sur quelques lépidoptères nouveaux, trouvés dans les Pyrénées Orientales en 1847. – Annales de la société entomologique de France **19**: 391–397.
- Hartig, F. 1937. I macrolepidotteri di Madonna di Campiglio. – Memorie della Società Entomologica Italiana **16**: 232–271.
- Henriksen, H.J. & I. Kreutzer 1982. The butterflies of Scandinavia in nature. – Skandinavisk Bogforlag, Odense, Denmark. 215 pp.
- Hewitt, G. M. 2000. The genetic legacy of the Quaternary ice ages. – Nature **405**: 907–913.
- Higgins, L. G. 1975. The classification of European butterflies. – Collins, London. 320 pp.
- Holdhaus, K. 1954. Die Spuren der Eiszeit in der Tierwelt Europas. – Abhandlungen der zoologisch-botanischen Gesellschaft in Wien **63**: 1–493.
- Hormuzaki, C. von 1901. Ueber die in den Karpaten einheimischen Arten der Gattung *Erebia* Dalm. Und deren Beziehungen zur pleistocänen Fauna Mitteleuropas. – Deutsche entomologische Zeitschrift *Iris* **15**: 353–380.
- ICZN 2000. International code of zoological nomenclature, fourth edition. – Natural History Museum, London. 126 pp.
- Jakšić, P. 1988. Privremene karte rasprostranjenosti dnevnih leptira Jugoslavije (Lepidoptera, Rhopalocera). – Societas Entomologica Jugoslavica, editiones separatae **1**: 1–216.
- Korshunov, Y. & Gorbunov, P. 1995. Butterflies of the Asian part of Russia. A guide. – Ekaterinburg. 202 pp.
- Kostrowicki, A. S. 1969. Geography of the Palearctic Papilionoidea (Lepidoptera). – Drukarnia Uniwersytetu Jagiellońskiego, Kraków. 371 pp.
- Krzywicki, M. 1966. Klucze do oznaczania owadów Polski, XXVII (Lepidoptera), 63 (Satyridae). – Państwowe Wydawnictwo Naukowe, Warszawa. 41 pp.
- Krzywicki, M. 1982. Der gegenwärtige Stand der Tagfalterfauna Polens unter besonderer Berücksichtigung ihrer Bedrohung. – Nota Lepidopterologica **5**: 3–16.
- Kudrna, O. 1986. Butterflies of Europe. Vol. 8: Aspects of the conservation of Butterflies in Europe. – Aula-Verlag, Wiesbaden. 323 pp.
- Lafranchis, T. 2000. Les papillons de jour de France, Belgique et Luxembourg et leurs chenilles. – Collection Parthénopé, éditions Biotope, Mèze (France). 448 pp.
- Lattes, A., P. Mensi, L. Cassulo & E. Balletto 1994. Genotypic variability in western European members of the *Erebia tyndarus* species group (Lepidoptera, Satyridae). – Nota Lepidopterologica Supplement No. 5: 93–104.
- Lattin, G. de 1967. Grundriss der Zoogeographie. – Fischer Verlag, Stuttgart. 499 pp.
- Leraut, P. 1980. Liste systématique et synonymique des Lépidoptères de France, Belgique et Corse. – Société entomologique de France, Paris. 334 pp.
- Lesse, H. de 1951. Contribution à l'étude du genre *Erebia* (4^e note). Répartition de *E. pandrose* (Borkh.) et de sa sous-espèce *sthennyo* Grasl. dans les Pyrénées. – Vie et milieu **2**: 267–277.
- Lesse, H. de 1952. Contribution à l'étude du genre *Erebia* (7^e note). *Erebia sthennyo* Grasl. est-il une bonne espèce ? – Revue Française d'Entomologie **13**: 217–219.
- Manley, W. B. L. & Allcard, H. G. 1970. A field guide to the butterflies and burnets of Spain. – E. W. Classey Ltd, Hampton. 192 pp. & 40 pls.
- Moucha, J. 1959. Neueste Forschungsergebnisse über unsere Lepidopteren-Fauna und deren Bedeutung für die Lösung zoogeographischer Fragen in der Tschechoslowakei (Lepidoptera). – Acta faunistica entomologica musei nationalis Pragae **4**: 3–81.
- Nekrutenko, Y. P. 1990. Dnevnye babochki Kavkaza. Opredelitel'. Semeistva Papilionidae, Pieridae, Satyridae, Danaidae. [Butterflies of the Caucasus. A Guide. Families Papilionidae, Pieridae, Satyridae, Danaidae] – Naukova Dumka, Kiev. 215 pp. 32 pl. [In Russian]
- Penck, A. & E. Brückner 1909. Die Alpen im Eiszeitalter. 3 Teile. – C. H. Tauchnitz, Leipzig. 1199 pp.
- Peschke, R. 1920. *Erebia lappona* v. *roberti* Peschke. – Internationale Entomologische Zeitschrift **145**: 118–119.
- Reichl, E. R. 1992. Verbreitungsatlas der Tierwelt Österreichs. Band 1: Lepidoptera – Diurna, Tagfalter. – Forschungsinstitut für Umweltinformatik, Linz. 6 pp. 216 pl.

- Roos, P. & Arnscheid, W. 1976. Zur Verbreitung und subspezifischen Gliederung von *Erebia pandrose* Bkh. im Alpenraum (Lep., Satyridae). Beitrag zur Kenntnis der Erebien, III. – Nachrichtenblatt der Bayerischen Entomologen **25**: 119–123.
- Sala, G. 1996. I lepidotteri del compensorio gardesano. – Società Editoriale Multimediale, Salò (BS). 160 pp.
- Schmitt, T. & G. M. Hewitt 2004. Molecular biogeography of the arctic-alpine disjunct burnet moth species *Zygaena exulans* (Zygaenidae, Lepidoptera) in the Pyrenees and Alps. – Journal of Biogeography **31**: 885–893.
- Schmitt, T., G. M. Hewitt & P. Müller 2006. Disjunct distribution during glacial and interglacial periods in mountain butterflies: *Erebia epiphron* as an example. – Journal of Evolutionary Biology **19**: 108–113.
- Schönswetter, P., I. Stehlik, R. Holderegger & A. Tribsch 2005. Molecular evidence for glacial refugia of mountain plants in the European Alps. – Molecular Ecology **14**: 3547–3555.
- Stehlik, I. 2000. Nunataks and peripheral refugia for alpine plants during Quaternary glaciation in the middle parts of the Alps. – Botanica Helvetica **110**: 25–30.
- Stehlik, I. 2003. Resistance or emigration? Response of alpine plants to the ice ages. – Taxon **52**: 499–510.
- Tatarinov, A. G. & M. M. Dolgin 1999. Bulavousye češuekrylye. In: A. Estafyev (ed): Fauna Evropejskogo severo-vostoka Rossii, To. VII, ch. 1. [Club-antenned Lepidoptera. In: A. Estafyev (ed): Fauna of the European north-east of Russia, Vol. VII, part 1.] – Nauka, Sanct-Petersburg, 183 pp.
- Thurner, J. 1964. Die Lepidopterenfauna Jugoslawisch Mazedoniens. I. Rhopalocera, Grypocera und Noctuidae. – Prirodnaučen Muzej Skopje, 159 pp.
- Tribsch, A. & P. Schönswetter 2003. Patterns of endemism and comparative phylogeography confirm palaeoenvironmental evidence for Pleistocene refugia in the Eastern Alps. – Taxon **52**: 477–497.
- Tuzov, V., P. Bogdanov, A. Devyatkin, L. Kaabak, V. Korolev, V. Murzin, G. Samodurov & E. Tarasov 1997. Guide to the butterflies of Russia and adjacent territories (Lepidoptera, Rhopalocera). Vol. 1. – Pensoft, Sofia-Moscow, 480 pp. incl. 79 pls.
- Varga, Z. 1971. Die Erebien (Lep.: Satyridae) der Balkanhalbinsel und der Karpaten III. Die Verbreitung und subspezifische Gliederung von *Erebia pandrose* (Bkh., 1788) nebst Beschreibung einer neuen Unterart: *E. pandrose ambicolorata* ssp. nova. – Acta biologica Debrecina **11**: 227–235.
- Varga, Z. 1975a. Zoogeographische Gliederung der Paläarktischen Orealfauna. – Verhandlungen des Sechsten Internationalen Symposiums über Entomofaunistik in Mitteleuropa: 263–385.
- Varga, Z. 1975b. Geographische Isolation und Subspeziation bei den Hochgebirgs-Lepidopteren der Balkanhalbinsel. – Acta entomologica Jugoslavica **11**(1–2): 5–41.
- Varga, Z. 1996. Biogeography and evolution of orealepidoptera in the Palaearctic. – Acta Zoologica Academiae Scientiarum Hungaricae **42**(4): 289–330.
- Verity, R. 1953. Le farfalle diurne d'Italia, vol. V. – Marzocco S.A., Firenze. pp. 124–226.
- Vila, M. J. R. Vidal-Romaní & M. Björklund, 2005. The importance of time scale and multiple refugia: Incipient speciation and admixture of lineages in the butterfly *Erebia triaria* (Nymphalidae). – Molecular Phylogenetics and Evolution **36**: 249–260.
- Warren, B. C. S. 1936. Monograph of the genus *Erebia*. – British Museum, London.
- Willien, P. 1990. Contribution lépidoptérique française à la cartographie des invertébrés Européens (C.I.E.) XVI. Le genre *Erebia* (Lépidoptères Nymphalidae Satyrinae). – Alexanor **16**(5): 259–290.
- Willien, P. & T. Racheli 1975. Description d'une nouvelle sous-espèce d'Italie de *Erebia pandrose* Borkhausen (Lep. Satyridae). – Entomops No **35**: 102–104.

Appendix

Tab. 1. Sampling sites and sample sizes. Listed from west to east approximately. --- = sampled at more than one locality. WD = sample size for male wing design. MG = sample size for male genital characters. FG = sample size for female genital characters.

nr	sample	massif or region	locality	country	WD	MG	FG
1	Pyrenees.C	Central Pyrenees	Gourette	F	50	31	5
2	Pyrenees.E	Eastern Pyrenees	---	And+F	41	39	3
3	Dauphiné	Dauphiné Alps	---	F	35	27	5
4	Pt.S.Bernh	Grajan Alps	Petit St. Bernhard	F	13	13	2
5	Gr.Parad	Grajan Alps	Valnontey	I	46	22	3
6	Penninic.N	Northern Penninic Alps	Wallis	CH	26	13	4
7	Penninic.S	Southern Penninic Alps	Val St. Barthélémy	I	25	40	2
8	Bernese	Bernese Alps	---	CH	34	28	5
9	Albula	Albula Alps	---	CH	50	30	5
10	Bernina	Bernina Alps	---	CH	22	24	5
11	Bergam.W	Western Bergamasque Alps	Pizzo Tre Signori	I	11	11	1
12	Bergam.C	Central Bergamasque Alps	Passo Vivione	I	32	28	1
13	Bergam.E	Eastern Bergamasque Alps	Passo Aprica	I	12	10	4
14	Ortler.W	Western Ortler Alps	Umbrailpass	CH	36	30	5
15	Ortler.S	Southern Ortler Alps	Gaviapass	I	45	38	5
16	Ortler.N	Northern Ortler Alps	Martelltal	I	14	14	0
17	Adamello	Adamello	Pso Croce Domini	I	32	32	5
18	Brenta	Brenta	Passo Grostè	I	50	36	2
19	Ötztal	Ötztal Alps	---	A	49	25	1
20	Karwendel	Northern Chalk Alps	Karwendel mountains	A	26	26	0
21	Rofan	Northern Chalk Alps	Rofan mountains	A	30	30	2
22	Lessinic	Lessinic Alps	Cima Carega	I	36	36	5
23	Dolom.Lat	Dolomites	Latemar	I	40	32	5
24	Dolom.Mar	Dolomites	Marmolada	I	23	16	5
25	Dolom.Pala	Dolomites	Pala	I	49	32	5
26	H.Tauern	Hohe Tauern	Gr. Glockner	A	44	33	4
27	Venetian	Venetian Pre-alps	Monte Cavallo	I	7	7	4
28	Carnic	Carnic Alps	Sappada	I	38	49	5
29	Amberg	Gurktal Alps	Amberg	A	13	13	2
30	Gerlitzten	Gurktal Alps	Gerlitzten	A	20	20	4
31	N.Tauern	Niedere Tauern	Tauernpass	A	42	33	2
32	Julian	Julian Alps	---	SLO	46	41	5
33	Sweden.N	Northern Sweden	Abisko	S	37	37	1
34	Norway.N	Northern Norway	Alta	N	37	37	5
35	Norway.S	Southern Norway	Dovre, On	N	44	44	4
36	Tatra	Carpathians	High Tatra	SK	28	21	5
37	Bucegi	Carpathians	Bucegi mountains	RO	28	20	1
38	Durmitor	Durmitor	Durmitor	XM	14	14	1
39	Rila	Balkans	Rila mountains	BG	10	12	2
40	Sevo	Apennines	Pizzo di Sevo	I	24	24	1
41	Altai	Central Altai	Kurai	RU	34	40	5
42	Sayan	Southern Sayan	Southern Tuva	RU	35	30	5
43	Narym	Southern Altai	Narym mountains	KZ	14	8	1

Tab. 2. Population means of the measured parameters. SP = number of spines per valve. OP = ocelli position. FWD = forewing design. HWD = hindwing design. AV = width antevaginal plate (mm). sd = standard deviation (for interval/ratio variables with adequate sample size).

Nr	Sample	SP	sd	OP	sd	FWD	HWD	AV
1	Pyrenees.C	2.113	1.0623	0.226	0.0193	2.12	2.63	1.17
2	Pyrenees.E	0.154	0.5150	0.274	0.0120	4.54	4.13	0.72
3	Dauphiné	0.111	0.2887	0.274	0.0293	4.00	4.52	0.81
4	Pt.S.Bernh	0.462	0.6279	0.277	0.0185	4.85	4.69	0.75
5	Gr.Parad.	0.091	0.2505	0.280	0.0157	4.46	5.06	0.81
6	Penninic.N	0.154	0.5547	0.269	0.0603	4.36	4.96	0.76
7	Penninic.S	0.400	0.6222	0.278	0.0414	4.48	4.72	0.78
8	Bernese	0.107	0.2841	0.278	0.0212	4.18	3.50	0.81
9	Albula	0.100	0.2754	0.281	0.0242	4.44	4.27	0.75
10	Bernina	0.042	0.1412	0.278	0.0214	3.52	4.07	0.76
11	Bergam.W	1.636	0.9244	0.212	0.0133	3.00	3.36	0.82
12	Bergam.C	1.196	0.7739	0.220	0.0310	2.75	3.57	0.73
13	Bergam.E	1.700	0.5869	0.232	0.0202	3.67	3.83	0.83
14	Ortler.W	0.117	0.2520	0.266	0.0184	4.36	5.00	0.69
15	Ortler.S	0.500	0.6778	0.259	0.0226	2.42	3.63	0.78
16	Ortler.N	0.179	0.5409	0.252	0.0261	3.14	4.57	--
17	Adamello	0.156	0.4295	0.259	0.0199	3.81	4.97	0.61
18	Brenta	0.292	0.5526	0.259	0.0242	2.10	3.39	0.80
19	Ötztal	0.260	0.4592	0.274	0.0320	4.08	4.65	0.80
20	Karwendel	0.135	0.5207	0.288	0.0260	3.92	3.96	--
21	Rofan	0.033	0.1826	0.290	0.1398	3.63	4.40	0.84
22	Lessinic	1.125	0.8650	0.238	0.0226	3.15	3.07	0.82
23	Dolom.Lat	0.484	0.7012	0.266	0.0196	3.25	4.59	0.77
24	Dolom.Mar	0.281	0.4820	0.262	0.0320	2.61	4.67	0.81
25	Dolom.Pala	1.813	1.3664	0.260	0.0248	3.47	3.31	0.78
26	H.Tauern	0.197	0.4667	0.264	0.0227	2.56	3.18	0.80
27	Venetian	2.286	0.9063	0.251	0.0107	1.86	2.86	0.83
28	Carnic	1.735	1.3961	0.248	0.0462	2.32	2.70	0.79
29	Amberg	0.115	0.2996	0.247	0.0323	4.00	4.50	0.61
30	Gerlitz	0.375	0.6463	0.274	0.0237	3.80	4.30	0.72
31	N.Tauern	0.197	0.3737	0.261	0.1586	4.16	3.33	0.73
32	Julian	1.634	1.1991	0.261	0.1034	3.78	3.42	0.89
33	Sweden.N	0.135	0.3466	0.237	0.0220	3.74	2.32	0.67
34	Norway.N	0.284	0.5075	0.259	0.0250	3.14	3.72	0.71
35	Norway.S	0.261	0.4510	0.248	0.0198	4.02	3.57	0.74
36	Tatra	0.119	0.3502	0.261	0.0169	4.75	5.93	0.74
37	Bucegi	0.000	0.0000	0.271	0.018	5.00	6.96	0.75
38	Durmitor	1.929	1.0535	0.231	0.0163	3.07	2.93	0.84
39	Rila	0.045	0.1508	0.275	0.0244	4.91	5.36	0.73
40	Sevo	0.021	0.1021	0.253	0.0276	4.37	4.04	0.87
41	Altai	0.125	0.3349	0.274	0.1711	5.02	5.53	0.79
42	Sayan	0.083	0.2306	0.281	0.0148	4.83	5.10	0.76
43	Narym	2.812	1.3076	0.275	0.0098	3.07	1.00	0.69

Tab. 3. Population means for SP, OP, FWD and HWD, rescaled to 0–100, and their rescaled sum. The populations (*pandrose* group only) are sorted according to increasing sum.

nr	sample	SP	OP	FWD	HWD	SUM
37	Bucegi	0	36	1	0	0
39	Rila	9	28	4	34	14
42	Sayan	17	17	7	40	15
41	Altai	25	30	0	31	17
5	Gr.Parad.	18	19	19	41	21
21	Rofan	7	0	48	55	26
36	Tatra	24	55	9	22	26
9	Albula	20	17	20	58	28
20	Karwendel	27	4	38	65	34
14	Ortler.W	23	45	23	42	34
6	Penninic.N	31	40	23	43	35
2	Pyrenees.E	31	30	16	61	36
3	Dauphiné	22	30	35	53	37
10	Bernina	8	23	51	62	38
8	Bernese	21	23	29	75	39
40	Sevo	4	70	22	63	43
19	Ötztal	52	30	32	50	45
7	Penninic.S	80	23	18	48	47
4	Pt.S.Bernh	92	25	6	49	48
17	Adamello	31	58	41	43	49
29	Amberg	23	81	35	53	55
31	N.Tauern	39	55	29	78	58
30	Gerlitz	75	30	42	57	59
16	Ortler.N	36	72	64	52	66
35	Norway.S	52	79	34	73	72
24	Dolom.Mar	56	53	83	49	72
34	Norway.N	57	58	64	70	75
23	Dolom.Lat	97	45	61	51	77
26	H.Tauern	39	49	84	81	77
33	Sweden.N	27	100	44	100	83
18	Brenta	58	58	100	77	91
15	Ortler.S	100	58	89	72	100